

Age of the micronektonic squid *Pterygioteuthis gemmata* (Cephalopoda: Pyroteuthidae) from the central-east Atlantic based on statolith growth increments

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Pterygioteuthis gemmata Chun, 1910 occurs worldwide in tropical oceanic waters except in the western Atlantic, Caribbean and Mediterranean Seas.^{1,2} This species is one of the smallest oceanic squids, with mature males and females attaining 25 and 32 mm mantle length (ML), respectively.² Paralarvae, juveniles and adults of *P. gemmata* are most common in epipelagic and mesopelagic waters of the tropical Atlantic. Their abundance is approximately similar to that of the predominant epi- and mesopelagic tropical squids, the micronektonic *Abraliopsis atlantica* (Enoploteuthidae), *Onychoteuthis banksi* (Onychoteuthidae) and planktonic cranchiids.³

The biology of *P. gemmata* is poorly-known. The hectocotylus of males lacks a chitinous hook which is found in the closely-related species *Pterygioteuthis giardi*; additionally in females only the right oviduct is functional.^{1,4} Because of frequent occurrence of both mature females and small paralarvae (1.3–1.5 mm ML), spawning of *P. gemmata* has been considered to take place in upper epipelagic layers of the Gulf of Guinea. Juveniles (> 100 mm ML) and adults make diel vertical migrations, ascending to the epipelagic water layers at night and descending into mesopelagic layers during the daytime.³

Age and growth rates in micronektonic oceanic squids have been studied by statolith ageing techniques in the enoploteuthids *Abraliopsis atlantica*, *Abraliopsis pfefferi* and *Enoploteuthis leptura* from the tropical Atlantic^{5,6,7} and *Abralia trigonura* from the North Pacific.^{8,9} The daily nature of growth increments within *A. trigonura* statoliths has been validated by statolith analysis in newly hatched paralarvae kept in aquaria.⁸ It has been found that all these enoploteuthids are rather slow-growing animals with life span of around 6 months.^{5,6,9}

The aim of this study was to estimate growth rates and maximum age of mature *P. gemmata* by statolith growth increment studies.

Ninety-five *Pterygioteuthis gemmata* of 10–32 mm ML were caught during the biological surveys of the orange-back squid *Sthenoteuthis pteropus* (Ommastrephidae) in the central-eastern Atlantic carried out by Russian research vessels 'Prognoz' and 'Ocher' in June–September 1985 and in September 1988. Samples were taken in open waters of the western part of the Gulf of Guinea (latitudes 2°15'N–3°30'S and longitudes 4°05'–15°W) off the Exclusive Economic Zones of African countries. Squid were caught at night (20–04 h) at depths of 25–300 m using the Russian zoological pelagic trawl RT/TM 33 type (vertical

opening 8–10 m) equipped with a 6 mm mesh liner. Squid were identified using the key elaborated by Nesis.² The dorsal mantle length was measured to the nearest 1 mm. Maturity stages were assigned from the scale developed for ommastrephid squids.¹⁰

Statoliths were removed from 12 maturing and mature females and 4 mature males with mantle lengths close to maximum known values for this species. Statoliths were then stored in 96% ethanol for further analysis in the laboratory using statolith-ageing techniques.¹¹ Total statolith length (TSL) was measured after Clarke.¹² From each pair, one statolith was ground, first the anterior side, then posterior side on a wet waterproof sandpaper (1500 grit) and embedded in Canada balsam. Growth increments were counted from the nucleus to the edge of the lateral dome by two observers using the eye-piece micrometer of a 'Biolam-R14' light microscope (magnification $\times 400$).¹¹ Statolith growth increments were well-resolved and similar in appearance and microstructure to daily growth increments of the enoploteuthid *A. trigonura*.⁸ Assuming them to be daily, the total number of growth increments in the ground statolith of *P. gemmata* was considered to be the age of the squid in days. Total number of growth increments for each specimen was obtained as an average of count numbers, if deviation between the average and counts was less than 5%.

Growth increments were observed in all ground statoliths of *P. gemmata* (Fig. 1A). They started depositing around a rounded nucleus with a diameter varying from 22 to 27 μm (mean 25 μm , $\text{sd} = 2.1$). Growth increments were the broadest in the lateral dome, and therefore they were measured and counted in this part of the statolith (Fig. 2). The first 30–40 growth increments lying outside the nucleus had a maximum width (4–5 μm). The width of successive growth increments gradually decreased toward the statolith margin to 2.5–2.8 μm . In the size range studied (21–30 mm ML), the total statolith length varied from 0.56 to 0.7 mm (mean 0.646 mm, $\text{sd} = 0.096$). Statoliths of *P. gemmata* adults were relatively large (mean 2.486% ML, $\text{sd} = 0.227$).

A minimum age of 47 days was observed both in a maturing female of 21 mm ML and a mature male of 22 mm ML. A maximum age of 77 d was revealed in a mature female of 30 mm ML (Fig. 2). Length-at-age data were described by a linear function:

$$\text{ML} = 13.43 + 0.1994 \cdot T \quad (R^2 = 0.7071),$$

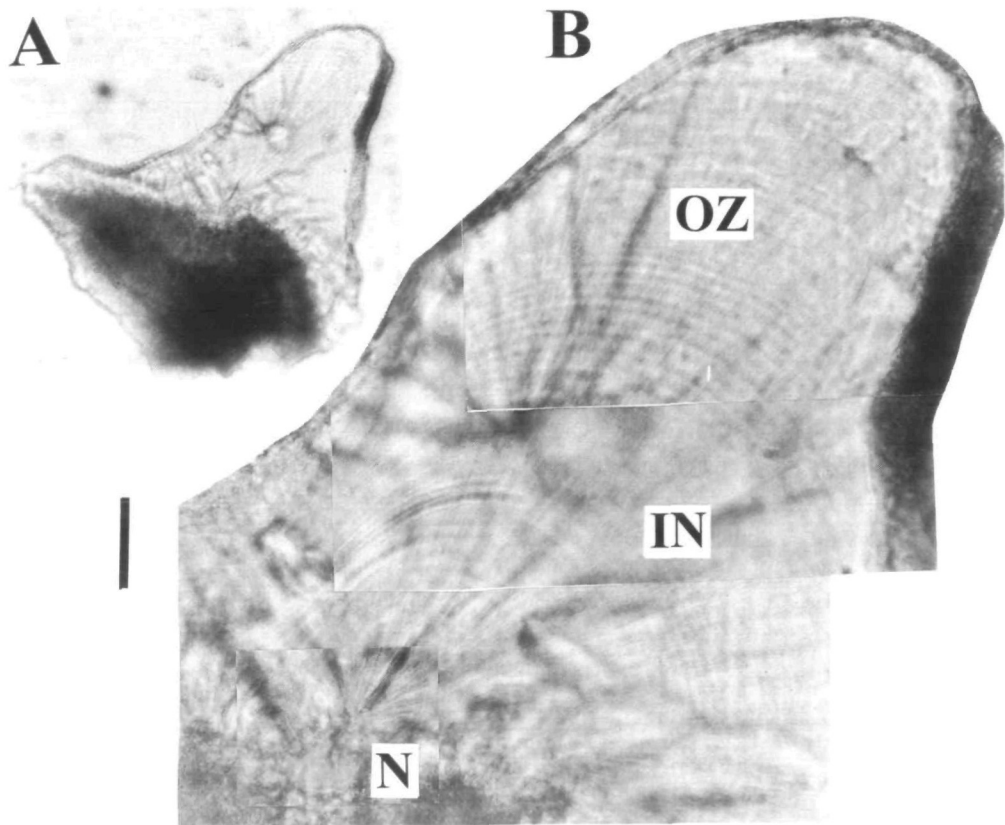


Figure 1 *Pterygioteuthis gemmata*. General view of ground statolith (A) and compound light micrograph of statolith of a maturing female (ML 23 mm) (B). Nucleus (N), inner zone (IN) and outer zone (OZ) of the statolith. Scale bar = 100 μ m for A and 25 μ m for B.

where ML is mantle length, and T is a number of growth increments in statolith.

Shortage of data did not permit the construction of separate growth curves for both sexes. However, sexual dimorphism in maximum ML (males attain 26 mm ML, whereas females attain 30 mm ML) suggests a lower growth rate of males at least in the mature ontogenetic phase. *P. gemmata* is a rather fast-growing squid. By the age of 70 d, males attain an average mantle length of 23–25 mm. At the same age, average sizes of females are 27–29 mm ML.

P. gemmata showed a difference between the sexes in the ages of maturation. Males were already mature at an age of 50 d, whilst females matured approximately two weeks later, with the oldest maturing female being 65 d old. All mature females were older than 62 d and had copulated. The hatching dates of our specimens ranged from May to August with a peak in July.

Statoliths of *P. gemmata* are quite similar in shape (well-developed lateral dome and short rostrum) to

those of another genus of the family Pyroteuthidae, *Pyroteuthis margaritifera* (Fig. 1).¹² The lateral dome of the *P. gemmata* statolith forms the anterior extension which is one of the characteristic features of the family Pyroteuthidae.¹³ The statolith microstructure of *P. gemmata* lacks distinct coloured growth zones observed in omastrephids¹⁴ and onychoteuthids (*Moroteuthis ingens*).¹⁵ As in squids of the closely related family Enoploteuthidae (*Abralia trigonura*, *Abraliopsis pfefferi*),^{7,8} statolith microstructure of *P. gemmata* is translucent, and growth zones can be distinguished mainly by increment width (broader increments in the inner zone and narrower increments in the outer zone). It seems probable that these two zones of fast and slow statolith growth correspond with two life history phases of *P. gemmata*. Paralarvae and small juveniles live continually in the superficial warm water layer, whereas juveniles > 10 mm ML start their diel vertical migrations.³ The same diel migratory patterns and consequent development of different microstructural

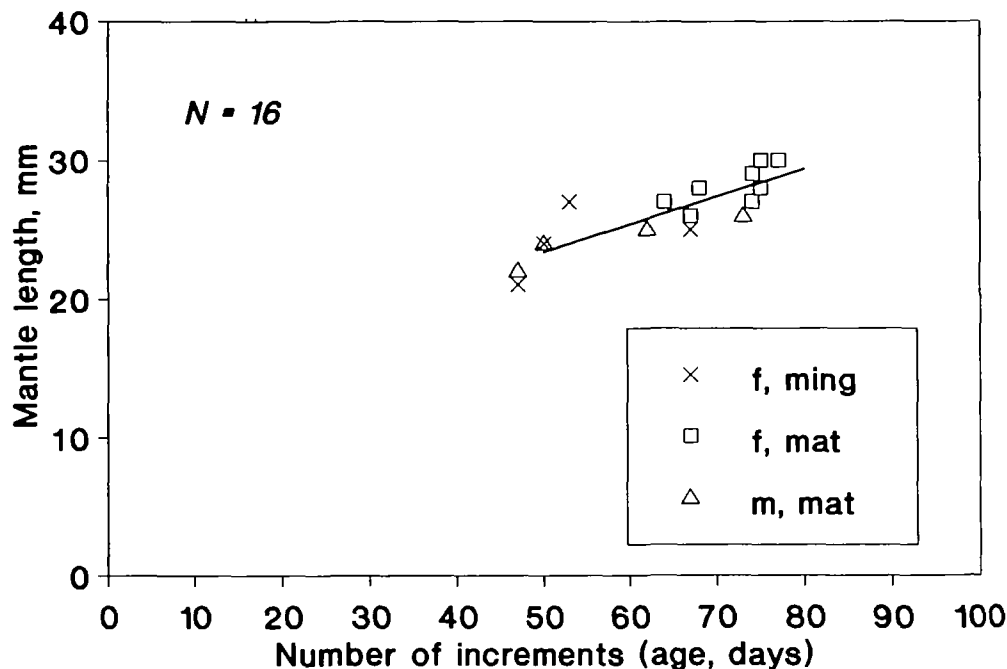


Figure 2. *Pterygioteuthis gemmata*. Relationship between number of statolith growth increments and mantle length.

zones has been noted in *Abraliopsis atlantica* and *Abralia trigonura*.^{5,8}

Pterygioteuthis gemmata seems to be the shortest-lived and most rapidly maturing squid among oegopsid squids.¹⁶ Taking into account the age of specimens with maximum-known ML, males mature at ages of 1.5 months and live up to 2.5 months, whereas females mature at 2 months and live up to 2.7 months. According to the data of Laptikhovsky,¹⁷ the development of *P. gemmata* eggs is rather fast (about 10 d) due to their small size and high ambient temperatures. Thus, the total life span (including time of egg development) of *P. gemmata* lasts about 3 mo. Similar longevity of the life cycle with rapid growth and maturation has been found in the small tropical sepoid *Idiosepius pygmaeus*.¹⁸ The high abundance of *P. gemmata* in the Gulf of Guinea Atlantic³ illustrates the successful life history tactics of these micronektonic squids (short life span, rapid growth and maturation, four recruitments per year) in the epipelagic and mesopelagic waters of the tropical Atlantic.

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Changes in mantle muscle structure associated with growth and reproduction in the tropical squid *Photololigo* sp. (Cephalopoda: Loliginidae)

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Squid mantle muscle tissue is predominantly made up of circular smooth muscle fibres, separated into blocks by thin ($\sim 30 \mu\text{m}$) bands of radial muscle fibres.¹ These smooth muscle fibres have helical myofibrils and are typically small; $< 10 \mu\text{m}$ diameter.² In many cephalopods circular muscle fibres are present in two structural states; mitochondria-rich and mitochondria-poor, analogous to fast and slow twitch muscle fibres in vertebrates.³ The bulk ($\sim 80\%$) of the mantle muscle tissue is made up of circular, mitochondria-poor muscle fibres. Growth of the mantle muscle occurs by the production of new muscle fibres and growth of existing fibres.⁴ Changes in the size structure of mantle muscle fibres and mantle muscle blocks are very extensive during growth of the animal.^{4,5}

Processes of senescence and reproduction can change the structure and appearance of the mantle muscle tissue. There is evidence that the mantle muscle tissue changes both in composition^{6,7} and structure^{8,9} during egg production; although there are exceptions.^{10,11} One of the most dramatic changes in the muscle tissue has been recorded in senescent cephalopods, in which the muscle fibres break down completely leaving only collagen fibres.^{12,13} Low lipid levels have been recorded in cephalopods and it is speculated that energy reserves may be stored as protein or carbohydrate¹⁴ in the muscle tissue, hence the changes observed.¹⁵

In this paper I describe the presence of nodes of disorganised circular muscle fibres in *Photololigo* sp. mantle muscle tissue. I then examined the relationship between the presence and extent of the nodes and the size and reproductive status of the animals.

Photololigo sp. is an inshore tropical loliginid squid species found along the central Queensland coast of Australia. The species used in this study is the most common in this region and in the past has been referred to by the specific name *chinensis* (Gray, 1849).^{16,17} However, recent taxonomic work

indicates that *chinensis* is the incorrect specific name.¹⁸ As this is one of two sibling species in the region, all individuals in this study were identified as being the same species using allozyme electrophoresis.¹⁸ *Photololigo* sp. lives for approximately 120 days and growth continues at a constant rate throughout its life.¹⁶

Fifty-one juvenile *Photololigo* sp. (2.5-49 mm dorsal mantle length) were caught using automated light-traps¹⁹ in the Townsville (North Queensland, Australia) region between October and January of the 1991/92 austral summer. Ninety-eight adult *Photololigo* sp. (60-150 mm dorsal mantle length) were caught in the same area using pair otter trawls (40 mm mesh) between August and November 1991 and in March 1992.

Dorsal mantle length (mm) of each individual was recorded before mantle muscle tissue was fixed for histological analysis. Juveniles were fixed whole and a sample of muscle tissue was removed later. Adults were killed by chilling and a sample of dorsal mantle muscle tissue was taken anteriorly, level with the locking mechanism. All muscle tissue was fixed in a formalin-acetic acid-calcium chloride solution (10 ml 37% formaldehyde, 5 ml glacial acetic acid, 1.3 g calcium chloride (dihydrate); distilled water to 100 ml). Fixed tissue was transferred to 70% ethanol 48 hrs before processing in paraffin wax. Muscle tissue was dehydrated through an ascending isopropanol series, cleared in chloroform and infiltrated with paraffin wax (Paramat). Tissue blocks were sectioned at $7 \mu\text{m}$, decerated in xylene and hydrated through a descending ethanol series. Histological sections were stained with Mallory-Heidenhain trichrome stain. Sections of muscle tissue were examined at 160x and 400x. Muscle tissue was sectioned longitudinally, so circular muscle fibres, ie. those muscle fibres that encircle the muscle mass, were cut transversely and radial muscle fibres longitudinally.⁴